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Avoidance of roads by large herbivores and its relation to disturbance intensity

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Abstract

Avoidance of roads has been demonstrated for many animal species, but little is known about the relationship between anthropogenic disturbance levels and the degree of avoidance by animals. We investigated the hypothesis that the strength of road-avoidance behaviour increases with the intensity of the disturbance for a large, disturbance-sensitive herbivore: the forest-dwelling caribou *Rangifer tarandus caribou*. We assessed the behaviour of 53 global positioning system-collared caribou monitored during the gradual modification of a highway over a 7-year period, while controlling for potentially confounding factors. We studied caribou movements, resource selection and distribution before, during and after road modifications at multiple scales. We expected that the degree of avoidance would be positively related to road width, traffic density and the presence of active construction sites. The proportion of individuals that excluded the highway from their home range increased as highway modifications progressed. A lower proportion of caribou locations was found in a 5000 m road-effect zone during and after highway modifications compared with before. Within that zone, caribou avoided habitat types that were selected at the home range scale. Caribou displayed higher movement rates in the vicinity of the highway, especially when traffic density was high. Our data support the hypothesis that avoidance of roads by large herbivores is positively related to disturbance intensity. Our results shed light on the behavioural mechanisms determining avoidance of human infrastructure by large herbivores, and suggest that increased human activity may affect behaviour at multiple scales. Conservation efforts in areas where roads are constructed or modified should be directed towards maintaining access to critical habitat resources, while also restoring habitat quantity and quality.

Introduction

Many human infrastructures influence the survival (Gibbs & Shriver, 2002), reproduction (Gerlach & Musolf, 2000), dispersal (Shepard *et al*., 2008), predator–prey interactions (Rogala *et al*., 2011) and behaviour (May *et al*., 2006) of animals. The North American road network, for example, covers more than 8 million km, and its development shows no sign of slowing (Forman *et al*., 2002). Each year, roads are improved worldwide to allow for greater traffic densities, and new roads are created in previously pristine wildlife habitats. Roads may be complete barriers to small animals (Shepard *et al*., 2008), and certain road widths (Smith-Patten & Patten, 2008) or traffic densities (Gagnon *et al*., 2007) may partially disrupt movements for larger species. Large animals are more likely to be negatively affected by roads, because their vagility and use of large home ranges increase their probability of interacting with roads (Gibbs & Shriver, 2002). Long-lived species with low reproductive rates are also the most vulnerable to road effects (Rytwinski & Fahrig, 2011), because their populations are less able to recover from high mortality rates caused by roads, both directly (e.g. road collisions) and indirectly (e.g. increased predation risk).

Many studies have highlighted negative impacts of human infrastructure on the behaviour of large herbivores. Caribou *Rangifer tarandus* consistently avoid paved and forestry roads (Leblond *et al*., 2011), seismic lines (Dyer *et al*., 2001) and tourist resorts (Vistnes & Nellemann, 2008) by several kilometres. Mountain goats *Oreamnos americanus* were unable to cross a highway in Montana at high traffic densities, and showed behaviours indicative of fear (e.g. running, erected tail and hair) even in the absence of vehicles (Singer, 1978). Moose *Alces alces* in Québec had higher movement rates in the vicinity of a highway, up to 3 h before and after crossing (Dussault *et al*., 2007). The level of disturbance associated with human infrastructure, however, is difficult to assess and their frequent association with other features (e.g. buildings are found near access roads) may confound our ability to disentangle their individual impacts on animal behaviour. Although the avoidance of human infrastructure by large herbivores has been demonstrated in many systems, we know little about the relationship between disturbance levels associated with these infrastructures and their relative degree of avoidance by animals. Such knowledge would be of paramount importance to implement suitable mitigation and conservation measures of human activities for large herbivore populations.

We investigated the hypothesis that the strength of road-avoidance behaviour by animals increases with disturbance intensity associated with the road. We studied a species that repeatedly demonstrates strong reactions to anthropogenic disturbances, the forest-dwelling caribou *R. t. caribou*. Throughout its range, forest-dwelling caribou are subject to several sources of disturbance, of which roads have among the strongest adverse impacts on their distribution and behaviour (Dyer *et al*., 2002; Leblond *et al*., 2011). Caribou may avoid the road surface, but also a road-effect zone (*sensu* Forman *et al*., 2002) of at least 1250 m around paved roads (Leblond *et al*., 2011), possibly because of avoidance of traffic noises (Jaeger *et al*., 2005). Near roads, caribou reduce their food acquisition and increase their energy expenditure, and they tend to have higher movement rates and increased vigilance (Murphy & Curatolo, 1987). Although caribou react strongly to humans and human infrastructure, they were also found to be sensitive to low-disturbance human footprints in the landscape, such as abandoned seismic lines in Alberta (Dyer *et al*., 2001).

To relate the strength of avoidance of caribou to various levels of a disturbance, we studied a long span of spatio-temporally changing highway, therefore controlling for potentially confounding factors such as the surrounding habitat. Highway 175 in Québec, Canada, has undergone significant changes between 2006 and 2010, changing from a two-lane to a four-lane highway, more than three times wider than before. This highway intersects the Charlevoix caribou range, a threatened forest-dwelling caribou population of less than 85 individuals. We used a long-term telemetry programme performed throughout the gradual modification of the highway to assess caribou behaviour before, during and after highway modifications. We thus considered the highway as a dynamic disturbance of varying intensity. We used highway width, human activity on construction sites and traffic density as surrogates of disturbance intensity, expecting that a larger highway, higher traffic densities and the presence of active construction sites (with workers, large trucks and blasting) would result in stronger avoidance (or a wider road-effect zone) by caribou.

We predicted that the highway would have specific effects on caribou behaviour; caribou would cross the highway less than expected when compared with random movements across the landscape (Dyer *et al*., 2002), and caribou would travel through the road-effect zone at a higher movement rate (Dussault *et al*., 2007) because they would perceive this area as a risky environment (Frid & Dill, 2002). We also predicted that as the intensity of highway disturbance increased, the number of caribou crossings would decrease, and that the width of the road-effect zone for caribou would increase in the vicinity of active construction sites (Mahoney & Schaefer, 2002), after the enlargement of the highway, and when traffic densities were high (Gagnon *et al*., 2007).

Materials and methods

Study area

Our study area (approximately 7250 km^2) was located north of Québec City in the Laurentides Wildlife Reserve (between 47°10’ and 48°00’ N, and 70°30’ and 71°50’ W), Québec, Canada (Fig. 1). It received a heavy annual snowfall (average >350 cm) and was characterized by a mixture of coniferous and mixed forest stands, typical of the boreal region. Balsam fir *Abies balsamea* and black spruce *Picea mariana* dominated at higher altitudes, whereas valleys and low-lying sectors were covered with mixed and deciduous stands. The study area was approximately 56% forested, and 37% was covered by disturbed habitats, mostly clearcuts of different ages and roads.

Sampling design

The study area was intersected by Highway 175, of which 95.5 km crossed the caribou range. Modifications of the highway began as early as May 2006 and as late as June 2009, and lasted between 100 and 900 days (depending on local terrain conditions, Table 1). Within this period, the highway was widened from approximately 25 to 90 m. Construction sites within the caribou range averaged 7 km in length. There was activity on construction sites during both day and night, and throughout most of the year, with short stops during holidays or because of adverse weather conditions. All highway modifications were completed by the end of 2010. Hence, within a given year, caribou could interact with the highway before, during, and/or after its modification.

Caribou capture and telemetry

Between April 2004 and March 2010, we captured 53 adult caribou (37 F and 16 M) by net-gunning from a helicopter, and fitted them with global positioning system telemetry collars (models TGW 3600 and 4600, Telonics Inc., Mesa, AZ, USA) programmed to collect locations every 3 or 7 h depending upon the collar model. Capture and handling procedures were approved by Animal Welfare Committees (Ministère des Ressources naturelles et de la Faune du Québec and Université du Québec à Rimouski). We recaptured caribou at 1- or 2-year intervals to download location data and replace battery packs. Collars were equipped with a timer release mechanism and were programmed to drop at the end of the study.

Spatio-temporal data

We used digital forest maps (minimum mapping unit size = 4 ha for forest stands, 2 ha for non-forested areas) to determine land-cover types using ArcGIS 9.3 (ESRI Inc., Redlands, CA, USA). These vector maps were derived from aerial photographs taken in 1998 at the scale of 1: 20 000. We updated maps

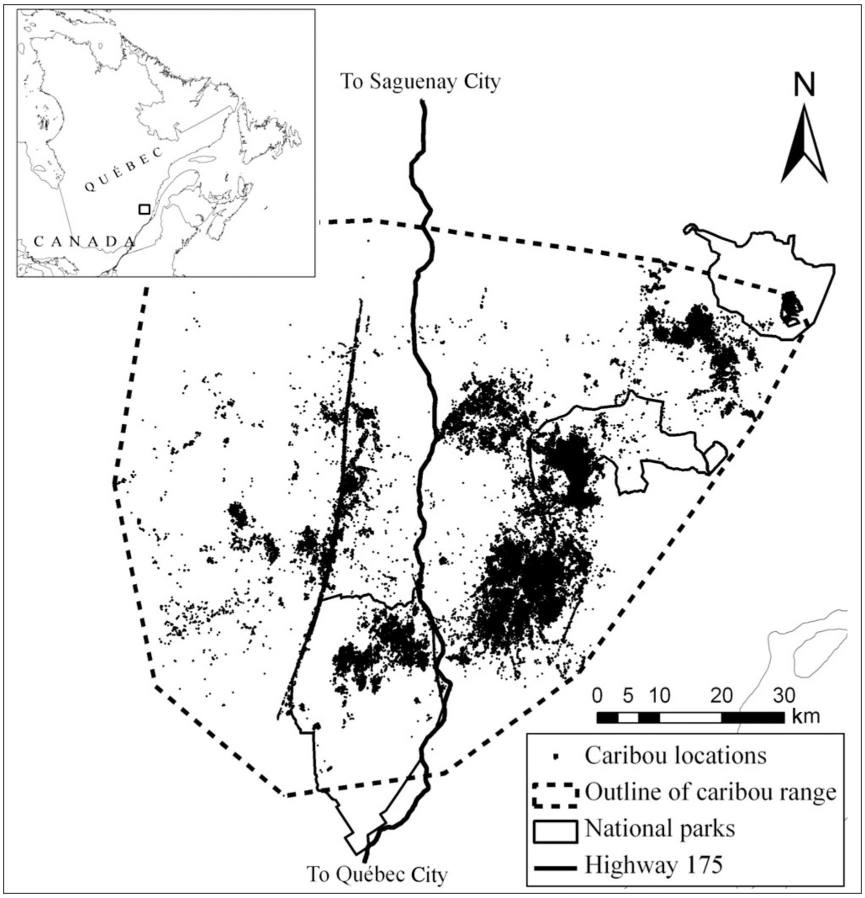

Figure 1 Map of the study area showing Highway 175 crossing the forest-dwelling caribou range in the Charlevoix region, Québec, Canada. Québec National park boundaries and caribou locations ($n = 364\ 100$) obtained with the global positioning system telemetry programme between 2004 and 2010 are shown.

Table 1 Length of Highway 175 segments crossing the forest-dwelling caribou range in the Charlevoix region, Québec, Canada, by highway status and year

	Highway status length (km)		
Year	Before highway modifications	During highway modifications	After highway modifications
2004	95.5	0.0	0.0
2005	95.5	0.0	0.0
2006	80.4	15.1	0.0
2007	80.4	15.1	0.0
2008	23.2	61.7	10.6
2009	0.0	80.4	15.1
2010	0.0	36.6	58.9

Highway modifications began in 2006.

each year to include new clearcuts, and combined available habitat types into 10 vegetation classes, including old mature conifer-dominated forests (conifer and mixed stands ≥90 years old; availability = 11.5% of the landscape), young mature conifer-dominated forests (conifer and mixed stands 50–90 years old; 31.0%), mature deciduous forests (>50 years old; 2.8%), recent clearcuts or natural disturbances (≤5 years old; 10.7%), old clearcuts or natural disturbances (6–20 years old; 10.5%), regenerating stands (generally 20–30 years after disturbance; 25.6%), open lichen woodlands (1.0%), wetlands (2.3%), powerlines (0.4%), and others (e.g. lakes, unproductive open lands; 4.2%). We used a digital elevation model with a 50-m resolution to measure local elevation and slope. We updated the map of the highway fortnightly to account for the spatio-temporal evolution of highway modifications and assigned a status to each 1-km road segment, that is either before, during or after road modifications.

We developed a mean hourly traffic index based on summary reports provided by the Ministère des Transports du Québec, which collected data using an electromagnetic traffic counter placed on the highway near the centre of our study area. We used a composite index based on the mean hourly traffic for the whole year, i (i.e. 24 different values of $\bar{\chi}_{\text{hour}}$, 1 for each hour), which we modified to consider relative variations in traffic density between months, j (12 different average values), and weekdays, k (7 different average values). We calculated the index using the equation:

$$\text{Traffic density} = \bar{\chi}_{\text{hour}_i} \times \frac{\chi_{\text{month}_j}}{\bar{\chi}_{\text{month}}} \times \frac{\chi_{\text{weekday}_k}}{\bar{\chi}_{\text{weekday}}}$$

The resulting index, varying between 18 and 786 vehicles per·hour, was assigned to every caribou location based on date and time. Because our index was collected on a single highway, it was independent from road width. This allowed us to overcome a bias often found in other disturbance studies comparing roads of different traffic densities (i.e. large roads are likely to have high traffic and vice versa).

Data analysis

Impacts of the highway on caribou behaviour

To determine if caribou crossed the highway less frequently than expected by chance, we simulated 1000 random highways by translating and rotating the actual highway in our study area to a new location within the caribou range (highway sections that fell outside of the range were deleted). *A posteriori* analyses revealed that the environment next to the real highway was not different from the environment around random roads. We counted the number of crossings of the random highway made by caribou along their movement paths, and performed one-sample *t*-tests comparing the mean annual number of random highway crossings per km to the observed annual number of crossings per km.

To determine if caribou increased their movement rate in the vicinity of the highway, we compared the movement rate (m h^{-1}) of caribou while crossing the highway (T0) to their movement rate a few hours before (five time-steps preceding T0, T-1 to T-5) and after (five time-steps following T0, T+1 to T+5) crossing (Dussault *et al*., 2007). We also created a continuous time variable increasing from 1 to 11 for each time-step, to take the non-independance of time series into consideration. We used a mixed effects linear regression model with movement rate as the dependent variable, time-step as the fixed effect independent variable, and crossing event (n = 93), individual (n = 12), time, and $time^2$ (i.e. based on our prediction that movement rate would increase near the highway) as random factors. We computed the least squares means of fixed effects and we performed multiple *post hoc* comparisons between the different time-steps using the Tukey's adjustment.

Impacts of increasing highway disturbance intensity on caribou behaviour

To determine if caribou avoided the highway, we assessed habitat selection by caribou at different spatial scales (i.e. landscape, home range and road vicinity). Our first step was to assess if caribou changed the location of their home range in the landscape according to the intensity of disturbance. To do so, we assessed the correlation between year (used as an approximation of increasing highway disturbance intensity) and highway density (km·km^{-2}) in annual home ranges (determined using the 100% minimum convex polygon) of individuals that included the highway at least 1 year. Similarly, we performed a Spearman correlation between the number of crossings per km per·individual of the highway and year to determine whether the number of caribou crossings decreased as highway modifications progressed.

To determine if caribou avoided the highway within their home range, we measured the minimal distance between each caribou location and the highway. We included this distance, along with 10 vegetation classes, elevation and slope, in a mixed-effect resource selection function (RSF) model (Manly *et al*., 2002). RSFs contrasted habitat features at observed locations with those found at a similar number of random locations drawn within the annual home range of caribou. We performed collinearity diagnostics and found that collinearity was low in our dataset (variance inflation value < 2). We set individual (year) as a random intercept to account for differences in sample size among caribou and for variation in selection among years. We included a second-order polynomial term for elevation, which was also centred on the mean to improve model fit. We used the predominant vegetation class, young mature conifer forests, as the reference category. We employed k-fold cross-validation to evaluate the robustness of our RSF (Boyce *et al*., 2002), and reported the average $\overline{r_S}$ resulting from 10 iterations. We included vegetation classes and topography as covariates because previous studies have outlined their importance to forest-dwelling caribou (see Leblond *et al*., 2011 for more details).

Although we predicted that the reaction of caribou would gradually increase with the intensity of highway disturbance, we also expected that this gradual response would be more easily observed within a given distance from the highway, likely determined by the perception range of caribou (Olden *et al*., 2004). Consequently, we assessed the impacts of disturbance level on caribou behaviour by constraining our analyses to a small fraction of caribou home ranges located in the vicinity of the highway. To do so, we used different road-buffer zones potentially representative of the perception range of caribou: 1250, 2500 and 5000 m. We explored larger road-buffer zones during preliminary analyses and obtained similar results with widths >5000 m and the global analysis using all caribou locations. By narrowing some of our analyses to the area close to the highway (our finest scale of analysis), we focused on the behaviour of individuals that did not exclude the highway from their home range. To determine if avoidance by caribou was higher near active construction sites and the larger highway compared with the unmodified highway, we evaluated RSF models of the same form as the global model using only the locations (observed and random) within the 1250-, 2500- or 5000-m road-buffer zones, and included interaction terms between minimum distance to the highway and highway status (before, during or after road modifications). In this analysis, we could not consider individual and year as random effects because of small sample sizes.

Although our RSF assessed the relative probability of caribou occurrence in relation to the highway, we wanted to evaluate the impact of disturbance intensity on the proportion of caribou locations within different road-buffer zones. We performed log-linear regressions to determine if the proportion of caribou locations within the 1250-, 2500- and 5000-m road-buffer zones was influenced by traffic density (with low and high values set below or above the median of 186 vehicles per·hour, respectively) or highway status (before, during or after highway modifications). We also performed a linear

Table 2 Annual number of crossings per km and crossings of Highway 175 by forest-dwelling caribou in the Charlevoix region, Québec, Canada, for each highway status

Year	Number of crossings per km (and crossings) of the highway				Mean number of crossings per km of the 1000 random highways ± standard deviation	*t*-value
	Before highway modifications	During highway modifications	After highway modifications	Total		
2004	0.14 (13)	–[a]	–	0.14 (13)	1.00 ± 2.13	12.83**
2005	0.21 (20)	–	–	0.21 (20)	1.19 ± 2.68	11.61**
2006	0.06 (5)	0.07 (1)	–	0.06 (6)	1.50 ± 2.93	15.47**
2007	0.16 (13)	0.07 (1)	–	0.15 (14)	1.87 ± 2.26	24.09**
2008	0.04 (1)	0.26 (16)	0.38 (4)	0.22 (21)	2.98 ± 3.89	22.44**
2009	–	0.01 (1)	0.07 (1)	0.02 (2)	2.16 ± 3.38	19.99**
2010	–	0	0.29 (17)	0.18 (17)	2.84 ± 3.91	21.53**
Total	(52)	(19)	(22)	0.97 (93)	14.17 ± 16.99	24.57**

The observed number of crossings per km was compared with the number of crossings of 1000 simulated (random) highways using *t*-tests.
[a]Highway status unavailable.
$^{**}P < 0.001$.

regression with movement rate as the dependent variable, traffic density as the independent variable and individual caribou ($n = 12$ caribou that crossed the highway) as a random factor, to assess if the movement rate was influenced by increased traffic density. We performed all statistical analyses using SAS 9.2 (SAS Institute Inc., Cary, NC, USA).

Results

Impacts of the highway on caribou behaviour

Only 12 (8 F and 4 M) of the 53 (23%) caribou crossed the highway at least once between 2004 and 2010, and only 93 of the 364 100 (<0.03 %) caribou locations were the end point of a movement step that crossed the highway. The annual rate of caribou crossings was much lower on the real highway than on random roads (Table 2). We observed a negative trend between the number of crossings per km per individual and year ($n = 7$ years; $r = -0.68$; $P = 0.09$).

The movement rate of caribou was higher during crossings of the highway (1011 m h^{-1} on average) than during time-steps just preceding or following crossing (≤683 m h^{-1}, Fig. 2). The movement rate of caribou was also higher during the two time-steps preceding (T-1 and T-2, 7.5 h before crossing on average) and the time-step immediately following the crossing (T+1, 3.5 h after crossing on average) compared with movement rates recorded at every other preceding and succeeding time-steps.

Impacts of increasing highway disturbance intensity on caribou behaviour

The correlation between highway density in caribou home ranges and year was negative ($r = -0.17$, $P = 0.03$). Eight out of nine individuals whose home range included the highway at least once during the study and that we monitored for ≥ 2

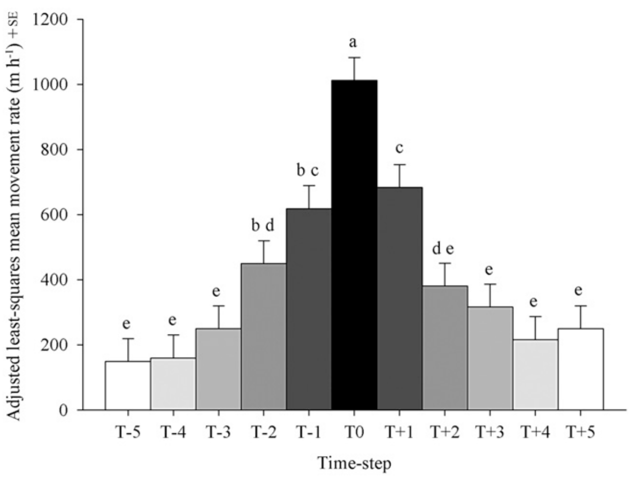

Figure 2 Adjusted least-squares mean movement rate [m h^{-1} + standard error (SE)] of forest-dwelling caribou during crossing of Highway 175 (T0), as well as five time-steps before (T-1 to T-5) and five time-steps after (T+1 to T+5), in the Charlevoix region, Québec, Canada, from 2004 to 2010. Bars sharing the same letter did not differ significantly.

years changed the location of their home range to avoid the highway at a large scale during (n = 3) or after (n = 5) its modification.

The RSF model using all caribou locations (Table 3) revealed that caribou avoided the highway at the home-range scale. Only 1713 (0.47%), 6974 (1.92%), and 16 067 (4.41%) locations were within the 1250-, 2500- and 5000-m road-buffer zones, respectively, which was 1.3–2.3 times less than random locations. Results from the RSF models focusing on the road-buffer zones showed that caribou generally avoided the highway even when they were in its vicinity (Table 3). Within these zones, they avoided all vegetation classes except power-lines and wetlands within 5000 m.

Caribou crossed the highway at a significantly higher movement rate when traffic density was high [1.60 ± 0.77 (standard

Table 3 Selection coefficients (β) and associated 95% CL of models of resource selection by forest-dwelling caribou in the Charlevoix region, Québec, Canada, from 2004 to 2010

	Within 1250 m of the highway (n = 1713) β (95% CL)	Within 2500 m of the highway (n = 6974) β (95% CL)	Within 5000 m of the highway (n = 16 067) β (95% CL)	All caribou locations (n = 364 100) β (95% CL)
Vegetation class[a]				
Old mature conifer	−1.11 (−1.37:−0.85)	−1.15 (−1.27:−1.03)	−0.48 (−0.55:−0.42)	0.31 (0.15:0.47)
Open lichen woodland			−1.04 (−1.80:−0.28)	1.90 (1.68:2.12)
Wetland	−0.23 (−0.57:0.12)	−0.25 (−0.49:−0.01)	1.01 (0.91:1.12)	0.90 (0.77:1.04)
Deciduous		−1.29 (−1.62:−0.96)	−0.77 (−0.94:−0.59)	0.43 (−0.07:0.93)
Young disturbance (<5 years)	−0.56 (−0.81:−0.31)	−0.55 (−0.69:−0.40)	−0.16 (−0.23:−0.08)	1.37 (1.18:1.56)
Old disturbance (6–20 years)	−1.28 (−1.82:−0.74)	−0.40 (−0.59:−0.22)	−0.41 (−0.52:−0.30)	0.34 (0.17:0.51)
Regenerating (>20 years)	−2.38 (−2.77:−1.99)	−2.10 (−2.28:−1.92)	−1.90 (−2.02:−1.78)	−0.87 (−1.04:−0.71)
Other	−3.27 (−3.82:−2.72)	−2.89 (−3.34:−2.44)	−0.80 (−0.95:−0.65)	−0.61 (−0.76:−0.46)
Powerline	2.29 (1.98:2.60)	2.46 (2.21:2.72)	2.23 (2.01:2.44)	4.28 (3.89:4.67)
Topography				
Elevation (km)	−5.86 (−7.51:−4.20)	−1.43 (−2.57:−0.30)	2.86 (2.42:3.31)	2.12 (0.69:3.56)
Elevation^2	130.05 (108.46:151.63)	75.95 (63.06:88.85)	17.11 (12.24:21.98)	5.80 (−0.61:12.22)
Slope (°)	−0.02 (−0.04: < 0.01)	0.05 (0.04:0.06)	0.04 (0.03:0.04)	−0.03 (−0.04:−0.02)
Distance to the highway				
Minimum distance to the highway (km)	0.57 (0.29:0.85)	0.82 (0.73:0.91)	0.04 (0.01:0.06)	0.03 (0.01:0.05)
Interaction between the minimum distance to the highway (km) and highway status[b]				
During highway modifications	−0.81 (−1.35:−0.28)	−0.14 (−0.27:−0.01)	0.05 (0.01:0.09)	
After highway modifications	−2.07 (−2.59:−1.54)	−2.95 (−3.30:−2.60)	−0.18 (−0.24:−0.12)	
Random effect [individual (year)]				0.11 (−0.08:0.31)
Validation (Spearman $\bar{r}_S$)	0.854	0.955	0.935	0.961

Models were first ran using all caribou locations (n = 364 100) and then using caribou locations within the road-buffer zones (1250, 2500 and 5000 m). Open lichen woodlands within 1250 and 2500 m, and deciduous stands within 1250 m were removed from the models because no caribou locations were observed in these classes. Results of model validation (Spearman's correlation $\bar{r}_S$ values) are provided.

[a]Reference category = young mature conifer-dominated stands.

[b]Reference category = before highway modifications.

CL, confidence limits.

Table 4 Parameter estimates (β) and associated 95% CL of the log-linear regression analyses assessing the influence of the interaction between traffic density or highway status and distance to the highway on the proportion of caribou locations within 1250-, 2500- and 5000-m road-buffer zones by forest-dwelling caribou in the Charlevoix region, Québec, Canada, from 2004 to 2010

	Within 1250 m of the highway		Within 2500 m of the highway		Within 5000 m of the highway	
	β	95% CL	β	95% CL	β	95% CL
Traffic density (reference category = low)						
High	0.25	0.16:0.35	−0.03	−0.08:0.01	<−0.01	−0.04:0.03
Highway status (reference category = before highway modifications)						
During highway modifications	−0.78	−0.91:−0.66	0.02	−0.03:0.07	−0.05	−0.08:−0.01
After highway modifications	−0.17	−0.29:−0.05	−1.48	−1.59:−1.37	−1.45	−1.55:−1.41

High and low traffic densities were set above and below the median value of 186 vehicles per hour of the traffic index, respectively.

CL, confidence limits.

error), P = 0.04]. Moreover, a higher proportion of caribou locations were found within 1250 m of the highway when traffic density was high, compared with when it was low (Table 4). We did not find a similar trend within 2500 and 5000 m of the highway. Caribou also used road-buffer zones less during and after highway modifications compared with before (although not significantly within 2500 m, Table 4).

Discussion

We investigated caribou reactions towards a single gradually modified highway, thereby controlling for potentially confounding factors, and our data support the hypothesis that avoidance of roads by large herbivores is positively related to disturbance intensity. The increased intensity of disturbance resulting from the wider highway, the presence of active construction sites, and higher traffic densities led to stronger behavioural reactions by caribou at several scales. The impacts of human activity on animal behaviour and distribution have been studied extensively in recent years (e.g. Hebblewhite & Merrill, 2008; Rogala *et al.*, 2011). However, to our knowledge, we are the first to relate the strength of avoidance shown by a mammal species towards a human infrastructure with the level of disturbance associated with that infrastructure.

At a broad scale, the few individuals that used the highway before road modifications gradually modified their space use to exclude it from their home range as the modifications progressed. The low number of annual highway crossings by caribou showed a decreasing trend ($P = 0.09$, low sample size) during the course of the study. At a finer scale, we found a lower proportion of caribou locations in the road-buffer zones during and after highway modifications as compared with before, showing that increased road disturbance resulted in stronger avoidance behaviour by caribou. Within these road-buffer zones, caribou avoided the habitat types that they selected elsewhere in their home range. The proportion of caribou locations in road-buffer zones did not decrease with increasing traffic density, as reported for other ungulate populations (e.g. Gagnon *et al.*, 2007), but rather translated into higher movement rates by caribou, which we also interpret as a reaction of caribou to increased disturbance. Although we considered the relative impacts of road width, human activity on construction sites, and traffic density separately, we underscore that these effects may occur simultaneously and act synergistically to influence the behaviour of large herbivores living in human-modified landscapes, thereby degrading habitat quality and landscape connectivity.

Caribou were already found to avoid infrastructure usually associated with little to no human activity, such as forestry roads, seismic lines, dams and pipeline corridors (e.g. Vistnes & Nellemann, 2008). Our results indicate that, even if caribou were reacting to increased disturbance levels, most individuals were using areas away from the highway before its modifications, suggesting that road disturbance had already shaped caribou distribution (May *et al.*, 2006). Individuals establishing their home range far from the highway likely showed the strongest road-avoidance. Therefore, the minimal disturbance intensity we measured (i.e. the unmodified two-lane highway with lowest traffic density) likely exceeded the threshold initiating a behavioural reaction for most caribou.

Animals face a conflicting trade-off when encountering a road: the strong incentive to access resources found on the other side of the road may be overcome by the perceived risks associated with vehicles and human activity. We found that 77% (41/53) of caribou did not cross the highway. It is likely that the individuals most sensitive to road disturbances were not able to access resources potentially available on the opposite side of the highway (including suitable areas protected by national parks). This represents a potential loss of 52–61% of the caribou range, for individuals west or east of the highway, respectively.

Animals generally mitigate the effects of the factors most detrimental to their fitness by avoiding them at broad scales (Rettie & Messier, 2000). As such, the highway was a determining feature for caribou when establishing their home range in the landscape (May *et al.*, 2006). For caribou, this may be a good strategy to increase survival: only three caribou–vehicle collisions occurred in our study area during our 7-year study. Our results suggest that the high disturbance levels found in the vicinity of the highway decreased habitat suitability up to at least 5000 m from it. As found with moose (Dussault *et al.*, 2007), caribou showed increased movement rates many hours before and after crossing, suggesting that a large disturbance zone around the road was perceived as risky, unsuitable habitat. This also suggests that, for most caribou, the perceived benefits of using resources up to 5 km away from the road were not strong enough to offset the perceived risks.

Despite the negative reactions we observed at the population level, some individuals may have benefited from living near the highway. For example, a few individuals may have selected sites to feed in the open terrain under powerlines adjacent to the highway, where abundant shrubs and herbaceous plants can be found. Proximity to the road may also result in lower predation risk for caribou (Muhly *et al.*, 2011). In the Greater Yellowstone Ecosystem (USA), Berger (2007) found that moose used the vicinity of roads to shelter from their traffic-averse predators. Given that individuals using the road-buffer zones reacted to increased disturbance, the perceived risks of living near roads for large herbivores could therefore surpass the former benefits following road enhancement projects or increased traffic levels.

Our study showed that the avoidance behaviour of a large, disturbance-sensitive herbivore is related to disturbance intensity. It may help to understand why sensitive species slowly disappear from fragmented, human-altered landscapes, adding to the global biodiversity decline. Conservation efforts in areas where roads are constructed or modified should be directed towards maintaining access to critical resources and restoring habitat quantity and quality. Although connectivity across the highway could be increased by constructing wildlife crossing structures (Olsson, Widen & Larkin, 2008), the strong avoidance behaviour shown by sensitive species like caribou could limit their effectiveness. In the case of a large or busy road, the wide road-effect zone might prevent individuals from finding and using the passages. To facilitate the adaptation of sensitive species to wildlife passages, we recommend to limit the intensity of human disturbances in their surroundings (e.g. by limiting human presence and vehicle noises; Clevenger & Waltho, 2005).

Our results suggest that the negative impacts of roads and increasing disturbance levels may affect animal behaviour over a wide range of scales. It may take several years after road modifications are completed to further evaluate their full impacts on animal behaviour. Time lags are common in studies assessing long-term impacts of human disturbances (Ewers & Didham, 2006), and forest-dwelling caribou were shown to display such delayed responses (Vors *et al.*, 2007). In the case of the Charlevoix caribou, if the wider four-lane highway eventually becomes a complete barrier to caribou movements, the population could be subdivided into two smaller groups, each having a greater risk of local extinction because of stochastic events (Hanski & Ovaskainen, 2003). We encourage further studies on road-avoidance behaviour to investigate whether behavioural impacts of human disturbances on wildlife may translate to impacts on population dynamics.

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